

FINAL REPORT

Title: Optimizing performance of
tree planting treatments after
severe wildfire

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Acronyms

NMDS — Non-metric multidimensional scaling

PReSET — Post-fire Reforestation Success Estimation Tool

Keywords

Conifer, Planting Success, Postfire, Priority Effects, Environmental Variation, Reforestation, Restoration, Seedling Mortality, Shrub Competition, Sierra Nevada, Silviculture, Yellow Pine–Mixed Conifer

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Abstract

Wildfires in the mid-elevation forests of California's Sierra Nevada mountain range have increased in size and intensity over the past half-century due to higher fuel loads from a century of fire suppression, together with longer fire seasons. The resulting large wildfires have produced larger high-severity patches (with near-complete tree mortality) than was historically typical in the Sierra Nevada. As a result, post-fire forest tree regeneration has become weak in many areas, leading forest managers to invest in tree planting as a strategy to hasten forest recovery after fire. Despite the critical importance of tree planting for forest recovery, it remains unclear how environmental variation influences active tree planting success relative to passive natural tree regeneration. To address this gap, we worked with the U.S. Forest Service to ask how variation in the abiotic environment (e.g., temperature, precipitation, light intensity, etc.), dispersal, and competition from shrubs impact tree planting success in the face of passive natural regeneration failure after forest fires throughout the Sierra Nevada. We report two main findings from this research. First, passive natural regeneration is lowest at the hottest, driest sites, and active tree planting can provide a moderate boost to forest recovery in these sites. Second, we found that the timing of tree planting matters, and that in some circumstances planting in the first year after wildfire is advantageous, but we also found that the importance of planting timing depends on the level of competition from shrubs. In places where shrub competition is intense, tree planting is much more successful if planting occurs during the year immediately following a fire (the soonest that it is usually practical to plant) and results in greater establishment of pine species. In contrast, in places where shrub competition is weak, delaying tree planting until some shrubs establish can facilitate tree seedling survival, perhaps by providing shelter from harsh conditions. Given the complex environmental controls of natural recruitment and planting success, we developed a web-based tool, using our results, that allows forest managers to identify high-priority active planting locations given the expected effects of tree planting.

Objectives

Our objectives were to measure tree seedling recruitment, growth, and survival in severely burned areas of yellow-pine and mixed-conifer forests in California's Sierra Nevada mountains, and to understand the drivers of its variation both in tree planting treatment areas, and in adjacent untreated areas. We addressed the following specific questions, as posed in our proposal for this project:

- 1) What is the optimal time to plant seedlings into severely burned areas?
- 2) How strongly does environmental variation influence natural and planted seedling regeneration?
- 3) How do tree planting methods (early planting, late planting, or no planting) and environmental conditions influence the species composition of re-establishing forests?

We successfully met these objectives and address each in greater detail below. Our study produced a dataset describing tree seedling density, growth, and survival in tree plantings after five fires, comprising 30–50, 11 m radius plots per fire paired across planted and adjacent unplanted areas.

Using these data, we created the web-based Post-fire Reforestation Success Estimation Tool (PReSET) to help forest managers predict planting success and prioritize planting locations (<https://reforestation.shinyapps.io/preset/>).

The project addressed the JFSP task statements for multiple Research Needs. To address Research Need 1, we tested relationships between the immediate post-fire environment (surviving tree species composition and location, topographic and site attributes), and the success of recovery actions (tree planting) by measuring tree planting effectiveness relative to background regeneration. We addressed Research Need 2, on the relationship between phasing of post-fire actions (tree planting and associated actions) and desired outcomes of tree density and species composition, by comparing the outcome of tree planting treatments implemented at different times after fire. The research results and the decision tool (PReSET) produced through this project also respond to Research Need 4 by assessing the relative effectiveness of alternative planting timing and by suggesting where these treatments should be prioritized on the landscape.

Background

Climate change is restructuring the controls on species distributions and species dominance in complex ways, resulting in ecosystems that operate outside of their historic range of variation (Walther et al. 2005, Parmesan 2006, Kelly and Goulden 2008, Bertrand et al. 2011, Stanton-Geddes et al. 2012, Zhu et al. 2012, Williams and Jackson 2016, Fei et al. 2017). The consequences of these changes range from benign to dramatic declines of many critical ecosystem services (Shaw et al. 2011, Carter 2013, Lee et al. 2015). Forests, especially, provide many ecosystem services such as timber, water filtration, fire regulation, and recreation (Krieger 2001, García-Nieto et al. 2013). While climate change can alter the distribution of species, range shifts and type conversions are often accelerated by anthropogenic changes to normal disturbance regimes (Vanderwel and Purves 2014, Serra-Diaz et al. 2015, Thom et al. 2017). In temperate regions, where forests provide \$900 billion per year of ecosystem services (Costanza et al. 1997), many biomes shift between forests, savannas, shrublands, and grasslands depending on climate and the frequency and intensity of disturbance (Bond et al. 2005, Bond and Keeley 2005, Bowman et al. 2009, Baudena et al. 2014, Lasslop et al. 2016). With changes in climate and disturbance regimes, shifts in forest biomes may result in steep losses of critical ecosystem services such as water provisioning and carbon storage (Núñez et al. 2006, Adams 2013, Thom and Seidl 2016, Sutherland et al. 2016). Given the rapid pace of human-caused environmental change, we need data to understand how climate and disturbance drive environmental change and ultimately how management can reduce losses in ecosystem services. In this study, we collected and analyzed field data from five California wildfires to evaluate factors influencing the success of post-wildfire tree planting, one of the most widespread and economically and ecologically important management interventions in western North America.

In forests adapted to low intensity disturbance such as yellow pine and mixed conifer forests of the North American Mediterranean-zone, extreme disturbance can lead to tree regeneration failure resulting in the conversion of forests to shrubland and a loss of ecosystem services (e.g., timber production, recreation, and cultural services; Safford and Stevens 2017). In this system, type conversion to shrubland often occurs as a result of fires that are now on average seven times larger in extent than the historical average and burn with much higher severity (Lenihan et al. 2008, Miller et al. 2009, Westerling et al. 2011, Safford et al. 2012, Miller and

Safford 2012, Safford and Stevens 2017), resulting in fewer surviving trees to produce seeds, which must then disperse much farther to support recruitment (Welch et al. 2016, Safford and Stevens 2017, Shive et al. 2018). Furthermore, while dispersal limitation can cause forest regeneration failure, forest regeneration can also be disrupted by changes in climatic averages and extremes (Young et al. 2019, Davis et al. 2019, Rodman et al. 2020), which can increase seedling water stress as temperatures increase and extreme weather becomes more common (Swain et al. 2018). To counter dispersal limitation and early establishment stress, forest managers often plant trees to overcome forest regeneration failure (Helms, J. A., and J. C. Tappeiner 1996, Brown et al. 2004). Tree planting is not consistently successful, however, and with the growth of exceptionally large fires, the amount of burned area that can be replanted is often limited by funding and other constraints (North et al. 2019). Because both passive tree regeneration and active tree planting outcomes are determined by complex and interacting processes, including seed dispersal, early abiotic stress, and competition from shrubs, scientists and managers have struggled to reliably predict outcomes (Davis et al. 2018). Identifying the mechanisms that control both passive natural tree regeneration and the success of active planting treatments is critical for sustainable and cost-effective forest management.

Patterns in seedling recruitment in burned forest areas can provide clues to where planting may be most efficient. In mixed conifer forests, tree regeneration in large, high-severity patches is often limited by low seed availability, since surviving trees are the main sources of seed. Dispersal from the patch edge drops to low levels within 50–100m (Irvine et al. 2009, Welch et al. 2016, Shive et al. 2018). When dispersal does not limit regeneration, seedling establishment can be limited by environmental factors that result in water stress, either by limiting precipitation or elevating heat load (Irvine et al. 2009, Welch et al. 2016, Shive et al. 2018). Furthermore, competition from shrubs can be harmful—competing for resources with tree seedlings in less stressful conditions—or beneficial—facilitating seedling survival by ameliorating harsh conditions (Callaway 1992, Irvine et al. 2009). Predicting how trees and shrubs will respond to the environment is difficult because of the complex interacting nature of environmental stresses and resources. In particular, greater water availability generally increases seedling establishment, but high productivity in wetter areas also produces intense competition from shrubs. Alternatively, in stressful, water-limited or low-nutrient environments, tree seedlings establish poorly, but seedling establishment may be aided by neighboring shrubs which provide shade, decrease water loss from wind, and stabilize soil. Therefore, active tree planting may be a priority in sites with intermediate environmental stress: sufficient stress such that natural regeneration is limited, but not so much stress that planted trees would also die (White and Long 2019).

In addition, conifer regeneration in mid-elevations of the Sierra Nevada has shifted in species composition (Welch et al. 2016). Historically, yellow-pine and mixed-conifer forests were dominated by fire-tolerant and shade-intolerant *Pinus* species such as *Pinus ponderosa* (ponderosa pine), and *Pinus jeffreyi*, (Jeffrey pine), which were well adapted to the historical fire regime (Welch et al. 2016, Safford and Stevens 2017). Conversely, fire-intolerant and shade-adapted species, such as *Abies concolor* (white fir), *Abies magnifica* (red fir), *Pseudotsuga menziesii* (Douglas fir), and *Calocedrus decurrens* (incense cedar), are increasing in representation as fire suppression has favored tree species with these traits. Tree planting practices typically seek to restore historically dominant species and where they succeed, they may shift tree composition toward its more historical, pine-dominated composition. Understanding how environmental variation and planting timing guides compositional development will provide managers with more detailed information to help guide planting efforts.

To address our objectives, we collected tree density data from post-fire tree plantings in severely burned patches across five wildfires in the Sierra Nevada mountain range. We used the data to ask how distance from a disperser, environmental variation (e.g., temperature, precipitation, solar radiation, elevation, etc.), and competition interact with seedling planting to determine tree density and thus recovery outcomes. Specifically, we asked:

1. How do the outcomes of passive natural regeneration and active reforestation vary along environmental gradients, including variation in climate, intensity of competition, dispersal, and topography?
2. Under what environmental conditions is active reforestation most likely to be effective and necessary for facilitating post-disturbance recovery, and how does this change with the timing of planting?
3. How does environmental variation and the timing of planting affect tree seedling composition, especially with respect to shade-tolerant and shade-intolerant conifer species?

Materials and Methods

We conducted this study in the yellow-pine and mixed-conifer forests (hereafter “mixed conifer forest”) of the Sierra Nevada mountain range in California, USA (Safford and Stevens 2017). The Sierra Nevada provides major ecosystem services to California in the form of timber, biofuels, water supply and filtration, carbon sequestration, and recreation (Shaw et al. 2011). Mixed conifer forest falls within 300 and 2400m elevation in the northern range and 1200 to 2800m in the southern range. Historically, the forest was dominated by ponderosa pine and Jeffrey pine, with sugar pine, white fir, and incense cedar as subdominants and was characterized primarily by low-density forests and woodlands (Safford and Stevens 2017), while wetter, cooler areas tended to support higher tree density (Stephens et al. 2020). Historically, these forests burned every 11–16 years with an average burn size of 200–400 ha. Starting in the early 20th century, fire suppression reduced fire frequency by 65–100% (Safford and Water 2014, Safford and Stevens 2017). This decrease in frequent fire led to a large (~250%) increase in stem density and a buildup of fuels (Safford and Stevens 2017). Higher fuel loads and greater fuel continuity, together with warming temperature and longer snow-free seasons, supported an increased average fire size of 1400 ha and a five-fold increase in high-severity fire (Safford and Stevens 2017). The forest type experiences a Mediterranean climate, with wet winters and dry summers. As in all mountain ranges, temperature and precipitation vary at relatively fine scales, driven largely by topography and elevation.

We compared planted and unplanted recovering forest land after severe forest fire. We sampled plots in five fires, all on land managed by the U.S. Forest Service (Fig. 1). Fires occurred between 1994–2008 and planting had occurred 1–3 years after fire (Table 1). We selected fires and planting sites within these age ranges so that (a) planting outcomes had at least 7 years to manifest and (b) records and/or institutional knowledge of past management were still reliable. We additionally selected fires that contained comparable planted and unplanted areas arranged along

<i>Fire</i>	<i>Year</i>	<i>Elevation (m)</i>	<i>Years Planted Postfire</i>
<i>Cottonwood</i>	1994	2250–2425	2, 3
<i>Power</i>	2004	1070–1735	3
<i>Moonlight/Antelope</i>	2007	1400–2000	1, 3
<i>American River</i>	2008	1630–2000	1, 2
<i>Piute</i>	2008	2100–2475	2, 3

Table 1. Wildfires included in the study with year, elevation range, and number of years after the fire that they were planted.

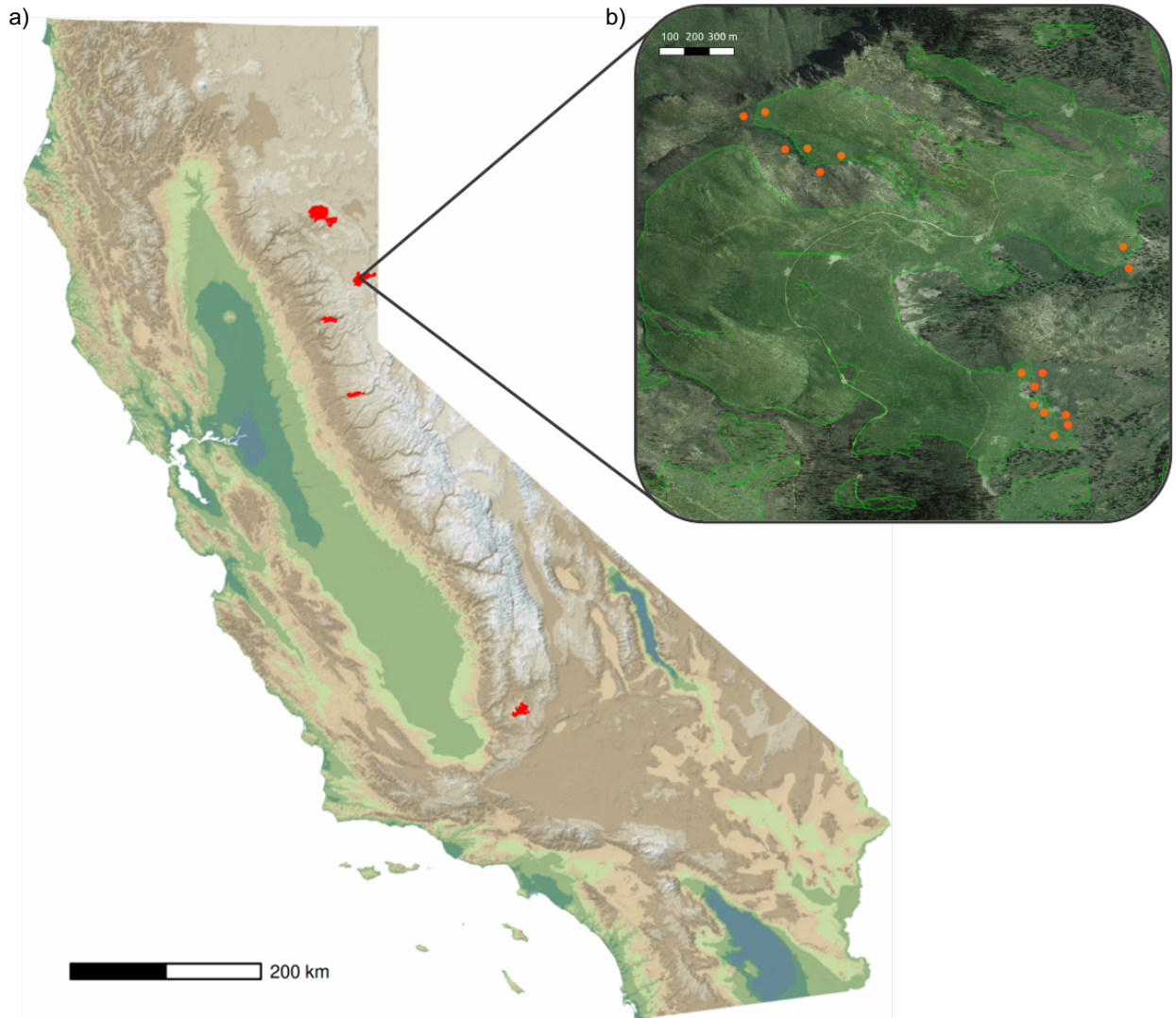


Figure 1. Locations of fires surveyed throughout the Sierra Nevada (a). Layout of paired plots along planting boundaries throughout a fire (b).

gradients in elevation and/or solar exposure (topographic aspect) that had received the same post-fire management (other than plantation management; see below in this section). Because passive natural regeneration is generally very weak (and thus active tree planting very important for forest recovery) far from seed sources (Welch et al. 2016), we prioritized data collection from planted areas within 150 m of seed sources in order to understand patterns and inform planting decisions in the more ambiguous zone where seed sources are present. For this purpose, we identified potential “seed source” distance coarsely by calculating the distance to the nearest non-high-severity patch of the fire (using USFS fire severity data; USDA Forest Service 2015) or the perimeter of the fire. We then measured actual seed source distance in the field; it sometimes differed substantially from the value inferred from severity maps, resulting in a sample dominated by plots with nearby seed sources but also including plots far from seed sources.

Study areas ranged in elevation from 1070 to 2475m, slope from 5 to 35%, average annual temperature from 6 to 13 °C, normal annual precipitation from 435 to 1815mm, and cloud-free

solar insolation in from 300 to 9900 Wh m⁻² day⁻¹. Our focal planting sites were planted with between 250 and 1200 trees per hectare (mean: 650), with trees characteristic of the site, typically including primarily ponderosa pine and Jeffrey pine, and sometimes also including sugar pine, Douglas-fir, white fir, and incense cedar, the latter four usually a small proportion of the planted trees.

Some sites included post-fire (pre-planting) salvage logging, pre- and/or post-fire reduction in shrub cover using chemical (herbicide) and/or mechanical (grubbing) methods, and/or replanting two to six years after initial planting where the original seedlings had died. Planted seedlings were nursery-grown and generally planted as one-year-old bareroot or container stock by hand crews using hoedads.

It was often not possible to distinguish planted from naturally recruiting tree seedlings in the field; therefore, we estimated the effects of tree planting treatments on the density of established tree seedlings by comparing planted and unplanted paired plots. To establish pairs, we identified high-severity areas within each fire using fire severity maps (USDA Forest Service 2015) and later confirmed that plots had experienced > 75% tree mortality by basal area in the field. We used the Forest Service Activities Tracking System (FACTS; USDA Forest Service 2018) spatial database of treatments, corroborated with information from forest managers when unclear, to locate the boundaries of planting treatments and other post-fire management. We restricted sampling to (a) high-severity burn areas, and (b) boundaries between planted and unplanted areas that were both forested prior to fire (as evidenced initially by aerial imagery and later confirmed in the field by presence of snags, logs, and/or stumps), did not coincide with any prominent natural features (e.g., ridgelines or transitions in substrate type), and experienced the same post-fire management (other than plantation-related management) according to the FACTS database. While planting unit boundaries often coincide with natural features (e.g., a fire severity boundary or transition to steep slope), we identified cases where boundaries were set arbitrarily (e.g., due to funding limitations, road access, or avoidance of cultural resources) and sampled along these non-ecological boundaries. To establish sampling points, we used a computer program to randomly generate pairs of plots along these boundaries separated by at least 50 m and usually more than 100 m. Within pairs, plots were located 50 to 75 m on either side of the planting unit boundary to buffer against edge effects and imprecise planting boundaries. In the field, we arbitrarily shifted plot locations up to 90 m parallel to the planting unit boundary if necessary to avoid anomalous sites (e.g., rocky outcrops).

Within each 11.3 m radius plot, we located and recorded every tree seedling > 25 cm tall and identified each to species, with the exception that ponderosa and Jeffrey pine seedlings were both recorded as “yellow pine” because they are often not feasible to distinguish as seedlings. If there were > 30 seedlings of a species (or yellow pine group), we instead sampled the seedlings of that species along a 22.6 m-long, 2 m-wide north-south transect through the middle of the plot, and we later estimated whole-plot density by multiplying by 8.87. We computed seedling densities based on the slope-area of the plot (as opposed to the horizontal area) because it may more closely reflect the growing area available to short-statured vegetation. To evaluate planting success, we specifically considered the density of the *planted* tree species (as opposed to all species present) in the paired planted and unplanted plots. In mixed-conifer forest, managers often aim to increase stocking density to 494 seedlings/ha (200 seedlings/acre) (Silvicultural Forest Handbook R5, USDA 1989). In addition, we visually estimated the percent of each plot covered by shrubs and average shrub height. We also measured litter and duff depth at four predetermined locations in each plot (and averaged them to obtain a plot-level average). To evaluate dispersal, we measured

the distance to the nearest seed sources (group of at least six reproductive conifers) using a laser rangefinder.

For each plot, we computed and/or extracted geophysical and climatic variables. We obtained elevation from 1 arcsecond (~30 m) resolution USGS 3DEP digital elevation models (DEMs) (USGS 2018), and we used these DEMs to compute slope (R package “raster”; Hijmans et al. 2020), topographic position index within a 2 km radius (R package “spatialEco”; Evans et al. 2020), topographic water index (R package “dynamtopmodel”; Metcalfe and Freer 2018) and cloud-free incoming shortwave solar radiation on the solstices (GRASS GIS function `r.sun`; Hofierka and Suri 2002). We also computed statistically downscaled mean annual daily minimum, daily maximum, and daily mean temperature for the 1981-2010 reference period at the ~30 m resolution of the USGS DEM based on TopoWx temperature layers (Oyler et al. 2015) at 800 m resolution. We performed downscaling using a modified gradient-inverse distance squared (GIDS) method (Nalder and Wein 1998) as implemented by Flint and Flint (2012), using a 4 km search radius and excluding latitude and longitude predictors to minimize artifacts associated with downscaling a grid (as opposed to interpolating between weather stations, the original GIDS application). Finally, we also obtained total annual precipitation data at 800 m resolution from the PRISM dataset (PRISM Climate Group 2019). We extracted all geophysical and climatic data at plot locations using bilinear interpolation.

Analysis

To evaluate the effect of environmental variation and timing of planting on establishment success, we tested predictor variables using a linear mixed effects model using the package ‘lme4’

Table 2. Predictors included in the global model and biologically meaningful interactions evaluated for improved model fit.

<i>Predictors</i>	<i>Interactions</i>
Mean Annual Temperature	Predictor * Planted
Mean Minimum Annual Temperature	Predictor * # of Years After Fire * Planted
Mean Maximum Annual Temperature	Mean Annual Temp. * Summer Solar Insolation
Normal Annual Precipitation	Normal Annual Precipitation * Summer Solar Insolation
Summer Solar Insolation	Mean Annual Temp. * Normal Annual Precipitation
%Forb Cover	Min. Annual Temp. * Normal Annual Precipitation
%Grasses Cover	Max. Annual Temp. * Normal Annual Precipitation
%Shrubs Cover	Min. Annual Temp. * Normal Annual Precipitation * Summer Solar Insolation
%Overstory Cover	Total Water Index * Normal Annual Precipitation
Average Shrub Height	Total Water Index * Summer Solar Insolation + Litter
Log10 Distance to Nearest Seed Source	Total Water Index * Elevation
Topographic Position Index	Topographic Position Index * Normal Annual Precipitation
Topographic Water Index	Topographic Position Index * Min. Annual Temp.
Elevation	Topographic Position Index * Elevation
Litter + Duff Depth	
Coarse Woody Debris	
Planting	
# Years After Fire Planted	

(Bates et al. 2019) in the statistical analysis program ‘R’ (R Core Team 2016). Because we have many possible predictors and are interested in potential interactions, we chose a modified backward-forward model-building approach focusing first on testing for interactions between single variable predictors and planting, and then testing for a pre-determined set of biologically meaningful two-way and three-way interactions between predictors (e.g., interaction between temperature and precipitation to represent the trade-off between water inputs and evapotranspiration; Table 2). To do this, we started with a global model that included all predictor variables and sequentially compared models with and without an interaction with planting for each predictor. Models were selected by comparing AIC; if AIC values for two models did not differ by at least 2, the simpler model was selected; otherwise, the model with the lowest AIC was selected. Only predictor-planting interactions that improved the model were retained. Because the outcome of competition can depend on priority effects (Fukami 2015), for competition-related predictors, we also tested for a three-way interaction between planting and the timing of planting. If an interaction between predictors improved the model, it was retained, and we subsequently compared models with and without a 3-way predictor-predictor-planting interaction. Finally, predictors were sequentially dropped from the model if they did not improve model fit by 2 AIC, since such predictors do not improve model performance much, and including them is likely to lead to overfitting the data. To meet model assumptions of residual normality and homoscedasticity, we added to the response variable (seedling density) the lowest non-zero density value observed and then transformed it using a natural logarithm (Ives 2015). Because the likelihood of dispersal decays exponentially with distance we used the base-10 logarithm of seed distance to approximate the rate of seed rain based on distance. To account for the nested structure of our data, we included a random intercept for each fire and nested pair ID within fire.

To evaluate the effect of environmental variation and tree planting on shade-tolerant versus shade-intolerant tree species composition, we used a generalized linear mixed effects model (Bates

<i>Predictor</i>	β	<i>std er</i>	<i>p</i>	Table 3. Model estimates, standard error, and p-value for each term in the final model predicting tree density. Continuous predictors were centered and standardized prior to fitting models to facilitate comparison of coefficients.
β_0	4.941	0.335	<0.00000	
<i>Topographic Position Index</i>	-0.198	0.072	0.00694	
<i>Elevation</i>	0.369	0.132	0.04212	
<i>%Shrubs</i>	0.990	0.342	0.00430	
<i>Year Planted</i>	-0.350	0.117	0.00337	
<i>Planting</i>	-1.750	0.374	0.00001	
<i>Min. Annual Temp.</i>	0.087	0.146	0.58114	
<i>Normal Annual Precipitation</i>	0.082	0.148	0.59078	
<i>Seed Source</i>	-0.232	0.064	0.00041	
<i>Litter + Duff Depth</i>	0.256	0.067	0.00019	
<i>Topographic Position Index:Elevation</i>	-0.183	0.062	0.00394	
<i>%Shrubs:Year Planted</i>	-0.455	0.133	0.00078	
<i>%Shrubs:Planting</i>	-1.155	0.474	0.01588	
<i>Year Planted:Planting</i>	0.403	0.148	0.00764	
<i>%Shrubs:Year Planted:Planting</i>	0.429	0.183	0.02016	
<i>Min. Annual Temp.:Normal Annual Precipitation</i>	1.160	0.180	<0.00000	

et al. 2019) with a binomial distribution to estimate the proportion of seedlings within each plot that represented shade-intolerant species (i.e., *P. ponderosa*, *P. jeffreyi*, and *P. lambertiana*) or shade-tolerant species (i.e., *A. concolor*, *A. magnifica*, *P. menziesii*, and *C. decurrens*). We followed the same model selection procedure as above to determine which predictor variables best predicted shade-tolerant versus shade-intolerant species. To capture overall community differences, we used non-metric multidimensional scaling (NMDS) to show the compositional differences that develop with tree planting. Because *P. ponderosa* and *P. jeffreyi* were difficult to distinguish from each other in the field, we grouped them for this analysis. We also only included conifers in this analysis because of their greater abundance and our focus on conifer regeneration. We conducted the NMDS using the ‘vegan’ package (Oksanen et al. 2019) in R. We chose NMDS as opposed to a constrained ordination (e.g., canonical analysis of principal coordinates) because it performed better during data analysis, was a simpler procedure, and resulted in similar patterns.

To translate the patterns we detected into geospatial predictions that are actionable by managers, we developed a web-based tool for predicting natural and post-planting seedling densities following new fires within our focal climate zone in the Sierra Nevada, subject to certain assumptions. The code and tool are hosted online at ‘<https://reforestation.shinyapps.io/preset>’. We identified post-fire shrub cover as an important predictor of seedling density (see Results), but because it is not known at the time of fire, we fitted an additional model to predict post-fire shrub cover (to in turn use as a predictor of seedling density) using only abiotic factors.

Results and Discussion

Results

Our selected models to predict tree density and species composition underscored the complex, multiple controls of recovering forest structure and composition. They included predictors representing climate, competition, dispersal, soil, and geophysical location (Table 3, 4).

<i>Predictor</i>	β	<i>std er</i>	<i>p</i>
β_0	4.258	0.889	<0.00000
<i>Normal Annual Precipitation</i>	-0.800	0.248	0.00126
<i>%Forbs</i>	0.381	0.232	0.10002
<i>Planting</i>	-4.767	0.820	<0.00000
<i>Year Planted</i>	-0.993	0.357	0.00534
<i>%Shrubs</i>	-0.839	0.269	0.00183
<i>Shrub Height</i>	-0.400	0.303	0.18679
<i>Overstory Canopy%</i>	-0.506	0.117	0.00002
<i>Topographic Water Index</i>	-0.408	0.183	0.02575
<i>Litter + Duff Depth</i>	0.189	0.300	0.52928
<i>%Forbs:Planting</i>	-1.922	0.693	0.00556
<i>Year Planted:Planting</i>	1.577	0.347	0.00001
<i>%Shrubs:Shrub Height</i>	-0.908	0.355	0.01041
<i>Litter + Duff Depth:Planting</i>	-0.713	0.322	0.02695

Table 4. Model estimates, standard error, and p-value for each term in the pine composition model. Continuous predictors were centered and standardized prior to fitting models to facilitate comparison of coefficients.

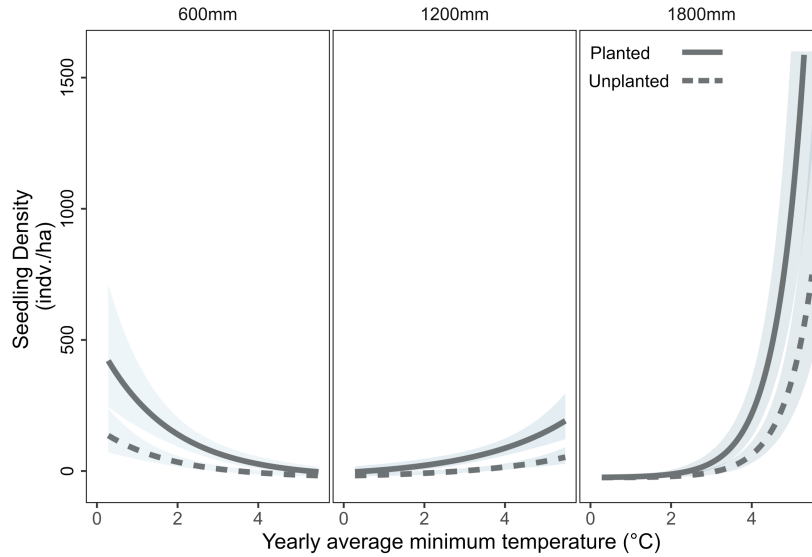


Figure 2. Predicted effect of average annual minimum temperature (°C) and normal annual precipitation (mm) on seedling density. To visualize the interaction between average annual minimum temperature and normal annual precipitation, the relationship between seedling density and annual minimum temperature is shown at low (600mm), moderate (1200mm), and high (1800mm) precipitation. Average

and normal annual precipitation (mm) did not interact with planting. All other factors in the model were held at their median value in the dataset. Back-transformed model predictions and standard error are shown.

For tree density, the effect of climate was best explained by an interaction between minimum temperature and normal annual precipitation ($\beta_{\text{int.}}: p = 2.11 \times 10^{-7}$) such that in the driest areas, tree density decreased with higher minimum temperature; at intermediate precipitation levels, tree density was independent of temperature; and in the wettest areas, tree density increased with temperature (Fig. 2). Tree planting did not interact with climate, suggesting that active planting increases tree density by a constant factor (relative to passive natural regeneration density) across climate gradients. For species composition, the proportion of pines occurring within plots decreased with normal annual precipitation and did not interact with planting (Fig. 3; $p = 0.001$).

Out of all the tested interactions between tree planting and environmental factors predicting tree density, only the interaction with shrub competition remained in the model. While the planting success depended on shrub cover, the number of years after fire that tree planting occurred determined whether shrub cover helped or hindered planting success. This was evidenced by a 3-way interaction between shrub cover, planting, and the number of years after fire that planting occurred ($\beta_{\text{int.}}: p = 0.042$). In unplanted plots, tree density moderately decreased with shrub cover. But in planted plots, tree density sharply increased with shrub cover if trees were planted the year directly after a fire, tree

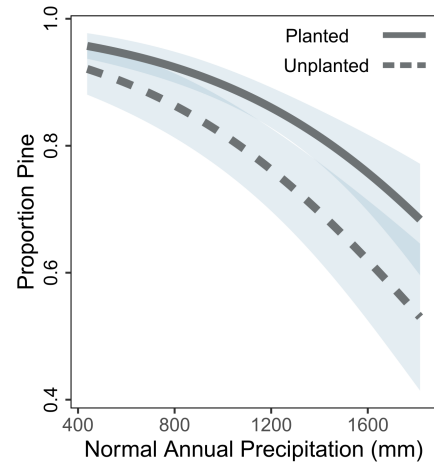


Figure 3. Predicted effect of normal annual precipitation (mm) on the proportion of species that are pines relative to all conifers. Normal annual precipitation did not interact with planting. All other factors in the model were held at their median value in the dataset. Model predictions and standard error are shown.

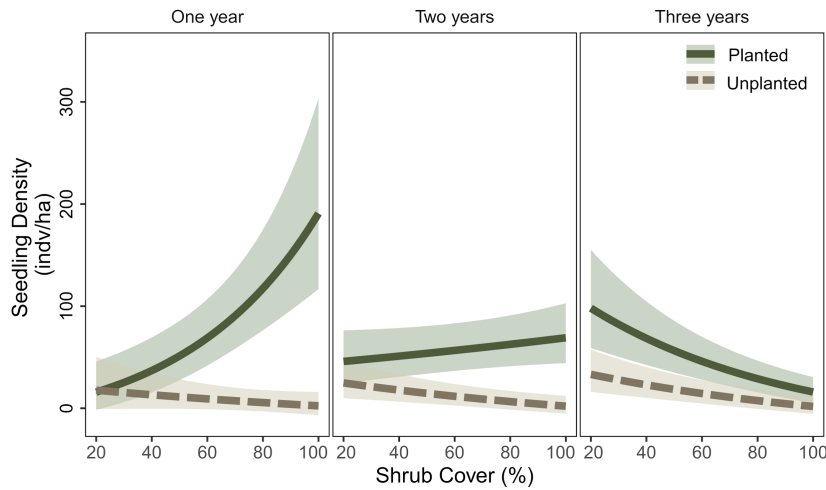


Figure 4. Predicted effect of shrub cover (%) and planting on seedling density for plantings one, two, and three years after fire. All other factors in the model were held at their median value in the dataset. Back-transformed model predictions and standard error are shown.

density moderately increased with shrub cover if trees were planted two years after a fire, and tree density increased moderately in the opposite direction as shrub cover decreased when planted three years after fire (Fig. 4)

For conifer species composition, the proportion of pines decreased with overstory canopy cover (Fig 5a; $p = 2 \times 10^{-5}$). Shrub cover and shrub height interacted in the model, such that the proportion of pines declined with shrub cover but only when shrubs were tall (Fig 6; $\beta_{\text{int.}}: p = 0.01$). Unlike tree

density, shrub cover did not interact with planting to influence species composition; however, forb cover did interact with planting such that the proportion of pines naturally decreased with forb cover without planting, but when planting did occur, forb cover did not impact composition (Fig. 5b; $\beta_{\text{int.}}: p = 0.0006$). And while year planted interacted with shrub cover to affect seedling density, the year planted only interacted with planting such that the proportion of pines was lowest without planting and increased the most when planted the year after fire and decreased with time since fire (Fig 5c; $p = 1.0 \times 10^{-5}$). In addition to climate and competition, seed source and small-scale

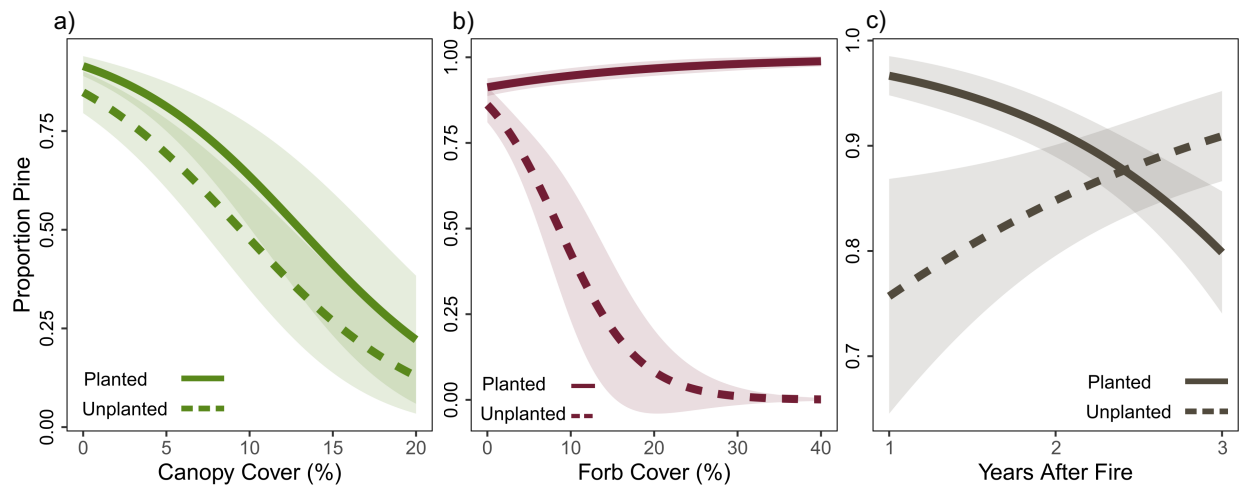


Figure 5. The effect of (a) overstory canopy cover (%), (b) forb cover (%), and (c) number of years after fire when planting occurs on the proportion of species that are pines relative to all conifers. Canopy cover did not interact with planting, but forb cover and years after fire did. All other factors in the model were held at their median value in the dataset. Model predictions and standard error are shown.

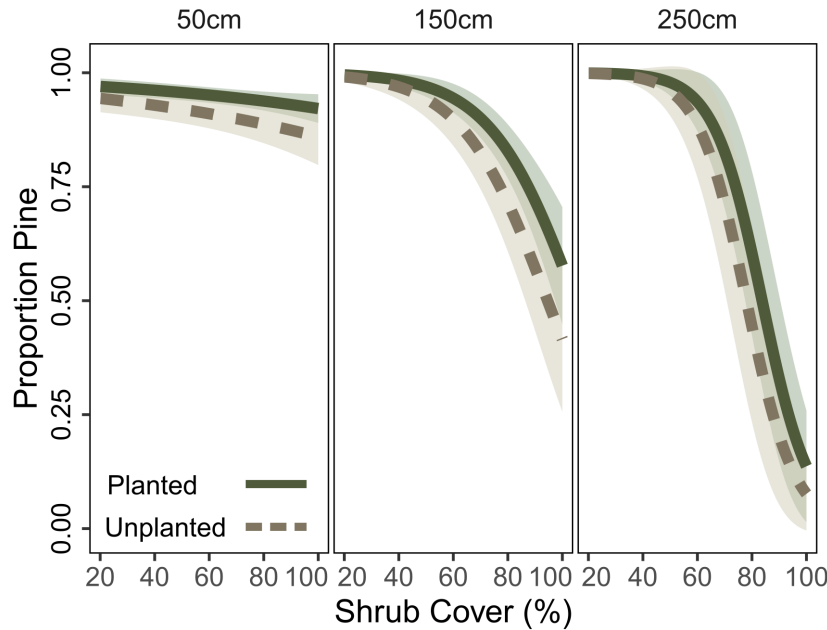


Figure 6. The effect of shrub cover (%) and height (mm) on the proportion of species that are pines relative to all conifers. To visualize the interaction between shrub cover and mean shrub height, the relationship between shrub cover and the proportion of pines is shown at low (50cm), moderate (150cm), and high (250cm) shrub height. Shrub cover and height did not interact with planting. All other factors in the model were held at their median value in the dataset. Model predictions and standard error are shown.

environmental conditions were associated with tree seedling density. Tree density increased with proximity to a seed source (Fig. 7; $p = 8.47 \times 10^{-4}$) and with increased litter and duff depth (Fig. 8a; $p = 5.66 \times 10^{-4}$). Topographic position interacted with elevation such that at low elevation, elevated topographic position moderately increases tree density, but as elevation increases, a greater topographic position becomes associated with decreased tree density (Fig 8b; $\beta_{\text{int.}}: p = 1.47 \times 10^{-3}$). For species composition, the proportion of pines was not affected by distance to seed source but did increase with topographic water index (Fig 9a; $p = 0.026$). The relationship of litter and duff depth with species composition depended on planting ($\beta_{\text{int.}}: p = 0.027$). As litter and duff increased, the proportion of pines observed decrease; however, this relationship disappears, and the proportion of pines is greater overall when planting occurred (Fig. 9b).

Without planting, stocking density targets (494 seedlings/ha) were rarely met, except in the warmest, wettest sites when all other factors were held at median values (Fig. 2). Planting sharply increased seedling density, but rarely increased seedling density to common stocking density goals (Fig. 2–5). The effect of tree planting on species composition at the community level resulted in more similar communities, which included more pines; unplanted areas included a higher representation of shade tolerant species (Fig 10).

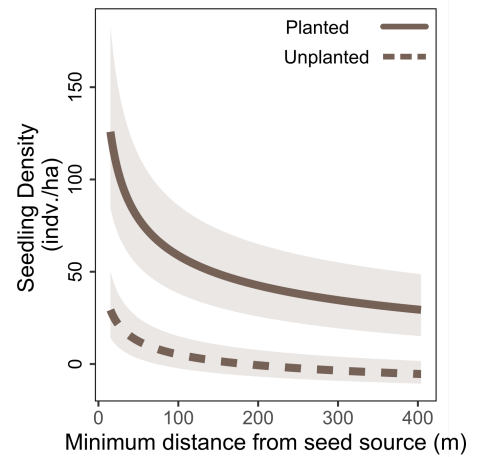


Figure 7. Relationship between minimum distance from a seed source (m) and seedling density. All other factors in the model were held at their median value in the dataset. Distance to seed source did not interact with planting. Back-transformed model predictions and standard error are shown.

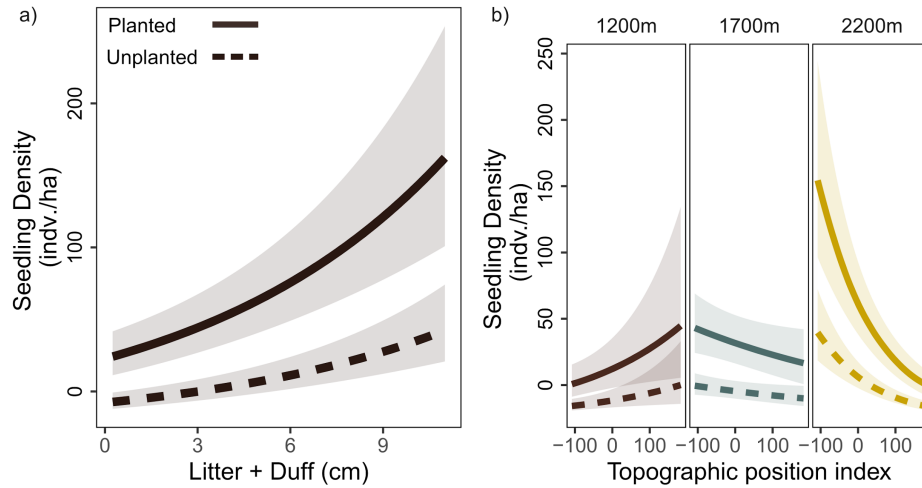


Figure 8. The effect of (a) litter and duff depth (cm) on seedling density, and the effect of (b) topographic position on seedling density depending on elevation. To visualize the interaction between topographic position and elevation, the relationship between seedling density and topographic position at

low (1200m), moderate (1700m), and high (2200m) elevation is shown. Litter and duff depth, topographic position, elevation did not interact with planting. All other factors in the model were held at their median value in the dataset. Back-transformed model predictions and standard error are shown.

Discussion

Our findings not only shed light on the biotic and environmental controls of tree seedling establishment and forest regeneration but also will help forest managers make more informed, cost-effective decisions to expand active tree planting as a tool to mitigate forest regeneration failure after large fires. As fires become more severe and the climate changes, understanding how the climate influences forest regeneration after large fires will be critical. Our results outline the climatic range in which tree planting will effectively increase regeneration. We also detail the complex relationship that planting success has with competition from shrubs and forbs. Our results suggest that areas with productive competing vegetation may be associated with failure of natural forest regeneration due to strong competition during the germination and early establishment stages. Forest managers can overcome the negative impact of intense shrub competition on regeneration by planting nursery-grown tree seedlings, thus bypassing the vulnerable germination and early seedling stages (Ledig and Kitzmiller 1992) and giving tree seedlings a head start in places where shrub competition is most intense. This strategy is only effective, though, when planting occurs the first or second year after a fire. If planting is performed more than two years

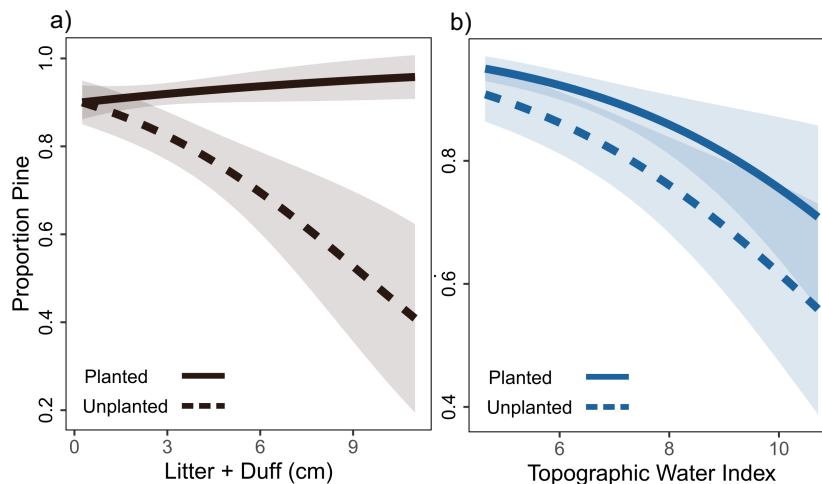


Figure 9. The effect of (a) litter and duff depth (cm), and (b) topographic water index, on the proportion of species that are pines relative to all conifers. Litter and duff depth did interact with planting, but topographic water index did not. All other factors in the model were held at their median value in the dataset. Model predictions and standard error are shown.

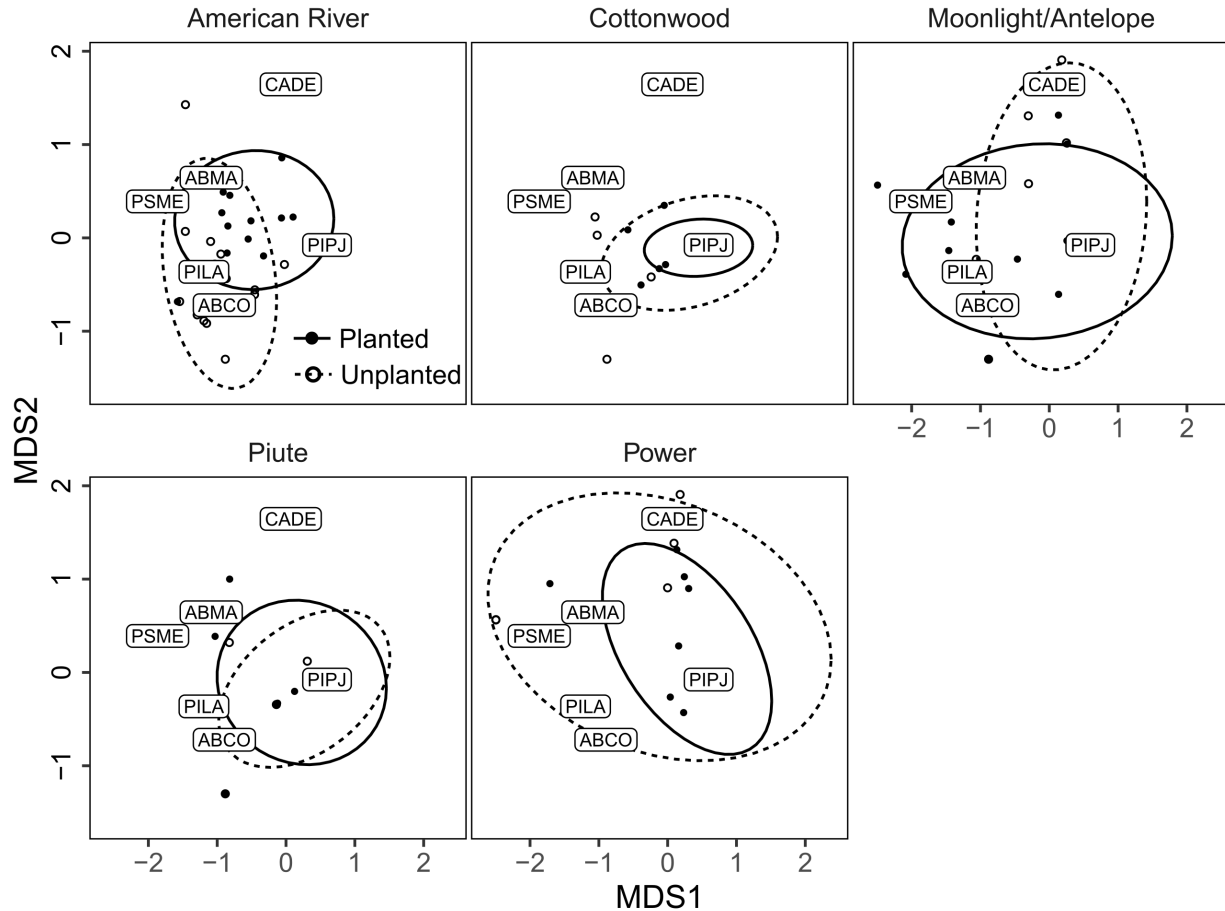


Figure 10. Conifer abundance-weighted community composition shown with non-metric multidimensional scaling (NMDS) using Bray-Curtis dissimilarity. All field plots were ordinated together but are displayed in separate panels for clarity. Species labels represent the centroid of that species in ordination space. Ellipses were calculated and drawn to encompass 80% of planted and unplanted ordination space. Stress = 0.13, $k = 2$.

following fire, shrub competition can substantially impact seedling survival, and it may become difficult to reduce through shrub control treatments (yet more important to do so). Furthermore, planting early can increase the proportion of pines in the regenerating community as well as overcome forb competition with pines. In addition, our results align with an established body of literature that shows that natural forest regeneration is strongest near a seed source, and they reinforce the importance of planting in places that are far from seed sources (Welch et al. 2016, Shive et al. 2018). While it did not interact with tree planting, we demonstrate that the topography plays an important role elevation and topographic position limit seedling establishment in positions where water is scarce.

Climate plays a strong role in determining tree density after a burn. Unsurprisingly, water availability is often seen as the most important determinant of tree density (Potito and MacDonald 2008). The interaction between normal annual precipitation and mean minimum annual temperature likely approximate water stress. Warmer areas require more water inputs to support tree densities to compensate for water loss from evapotranspiration. Tree seedlings with shallow roots are more sensitive to water loss, likely with mortality that tracks increased transpirational demand (Hanson and Weltzin 2000, Potito and MacDonald 2008). Surprisingly, we found that

active tree planting increases tree density by a constant factor across the precipitation and temperature gradients. This suggests that climate-related mortality likely occurs both at the earliest stages of recruitment (i.e., germination and early seedling establishment) and with more established seedlings (i.e., planted seedlings). This differential impact likely occurs because root establishment is critical for newly emerged seedlings and they are more sensitive to water stress, whereas planted trees have more established root systems and likely can extract deeper water to buffer against low rainfall and hot conditions (Hanson and Weltzin 2000, Potito and MacDonald 2008). Although active tree planting increases seedling density most under the climatic conditions where passive natural regeneration is strong, planting in harsher sites where natural regeneration is weak (and where planting increases tree densities less) may nonetheless be necessary for managers to approach or achieve target seedling densities. Climate also impacted species composition. As normal annual precipitation increased, the proportion of pines decreased, perhaps underscoring a tradeoff between competition and resilience to water stress or an increase in available niche space for more shade tolerant species. Planting increased the proportion of pines overall but did not change the relationship between precipitation and species composition.

These results suggest that active planting in hot, dry areas can work to increase tree density, at least in the near term. Given that natural regeneration tends to be low in hot, dry areas—as multiple studies including this one have found (Stevens-Rumann and Morgan 2019)—managers may want to consider longer-term climate-driven shifts in forest cover and prioritize planting in locations where the projected future climate will support sustainable forest tree recruitment into the future (North et al. 2019, Stevens-Rumann and Morgan 2019). Hot, dry areas where natural conifer regeneration is poor may be transitioning to oak woodlands and shrublands typical of lower elevations, potentially making planting strategies to maintain mixed conifer forest in these areas cost-ineffective (White and Long 2019, North et al. 2019). Identifying where mixed conifer is no longer suitable is complicated, though, because poor natural seedling establishment can be a response to other anthropogenic factors. In particular, unnaturally large and severe wildfires—a consequence of past fire suppression—often catalyze type conversion to montane chaparral or other vegetation (Welch et al. 2016, Airey Lauvaux et al. 2016). Thus, in those cases of passive natural recruitment failure, active tree planting may serve its intended function of restoring forests that would otherwise naturally exhibit resilience to high-severity fire.

At the same time, it is important to note that active tree planting in areas where passive natural regeneration is expected to be strong may not only represent a waste of resources: it may actually be ecologically counterproductive, producing dense stands with high tree-tree competition and elevated fire susceptibility (Kobziar et al. 2009, Zald and Dunn 2018). Thus, seeking to prioritize planting where it is most likely to bring naturally low seedling densities into an acceptable range is likely both ecologically and financially prudent. For instance, our results suggest that the warmest sites with relatively high precipitation may generally exceed stocking targets with passive natural regeneration alone, assuming a seed source is near (Fig 2.).

While active tree planting may produce a relatively constant proportional increase in seedling density across abiotic climatic gradients, our data show that understanding the balance between tree regeneration and shrub competition is critical for implementing successful tree planting. Naturally recruiting tree density declines as competition with shrubs increases (Welch et al. 2016). As a lifeform, shrubs resprout or germinate and grow more quickly and can therefore overtop tree seedlings, starving them of light and decreasing available soil moisture (Conard and Radosevich 1982, Lanini and Radosevich 1986, Oliver 1990, Plamboeck et al. 2008). Therefore, tree seedlings depend on growing conditions where shrub cover is not complete, and where tree

seedlings are provided an opportunity to overtop shrubs and outcompete or coexist with them. Our results suggest that forest regeneration (and plantation) failure can occur where tree seedling growth lags behind shrubs after fire. When trees were planted the year following a fire, planting dramatically increased tree density in the locations where shrub density ultimately would become high (i.e., indicative of fast shrub growth). Likely these areas provide ample resources for high productivity, which would support high tree seedling survival in the absence of shrubs; however, within natural systems, shrubs take advantage of these elevated resources more quickly than tree seedlings and outcompete them (Conard and Radosevich 1982, Lanini and Radosevich 1986, Oliver 1990, Welch et al. 2016). By planting trees in these areas early, managers give tree seedlings enough of a head start to establish, overtop shrubs, and survive. Therefore, the advantage of active tree planting in areas of high shrub productivity is strongest during the growing season after fire.

Surprisingly, in low-productivity areas, planting increases tree density most strongly three years after a fire. This may suggest a facilitation effect of shrubs on tree seedlings, as has been observed in Spanish Mediterranean-climate forests (Castro et al. 2002, Gómez-Aparicio et al. 2004) and dry sites in California (Callaway 1992). Given low shrub productivity at more stressful sites, tree seedlings may benefit from the effect of shrubs in moderating water loss by reducing wind and providing partial shade (Gómez-Aparicio et al. 2004, Irvine et al. 2009). Taken together, these results suggest that managers can take advantage of the tradeoff between competition and facilitation by adjusting the timing of planting. They will be most successful if they can predict where shrub cover (and thereby competition) will be greatest and target those areas for planting soon after a fire. In places where shrub growth is not vigorous, tree planting may actually benefit from waiting.

Of the trees surviving shrub competition, pines tend to occupy locations with more available light. Overstory cover and tall shrub cover decrease available light thereby reducing site suitability for shade-intolerant species, including pines. Forb competition may not have impacted overall seedling density, but it can shift the composition of species toward more shade-adapted species, possibly by increasing shade during establishment. Importantly, this suppression of pines can be overcome with planting, which likely overcomes the impact of shading by forbs.

Dispersal limitation in large, high-severity burned patches strongly limits tree recruitment (Welch et al. 2016, Shive et al. 2018), yet active tree planting increases seedling density regardless of the distance to a seed source. This suggests that even planting trees close to surviving seed sources can meaningfully increase seedling density. Given the multiple factors and complexity of controls on seedling density, perhaps it is unsurprising, because even microsites close to a seed source can face other impediments to natural regeneration, such as intense competing vegetation. It is thus useful to know that even in these sites where seed rain is presumably abundant, establishment limitations can be overcome with active planting. The wide standard error around the effect of distance to seed source and the moderate complexity of our final model suggest that dispersal limitation is only a part of what limits tree recruitment in mixed conifer forest after severe wildfire. Furthermore, distance to a seed source did not affect composition. Given the differences in seed production, mast year, size, and dispersal mode among conifers, the intensity of seed rain likely varies by species, which in theory, could translate to compositional differences with distance to a seed source. We did not, however, record distance to a mature individual for each species, and seed rain also depends on the abundance of the remaining tree species in addition to distance. It is possible that the effect of dispersal on species composition is more complex and requires more detailed data to elucidate dispersal-related patterns of composition.

In addition to climate, competition, and dispersal, our results show how the physical environment influences recruitment, likely through how it impacts water availability. First, a thicker litter and duff layer (as measured 10 to 24 years post-fire) is associated with greater seedling density, perhaps as a correlate of increased site productivity. In contrast, greater litter and duff depth was associated with a smaller proportion of pines under natural regeneration, but planting eliminated that relationship. The mechanism behind these relationships is difficult to establish with these data because litter and duff depth were measured years after planting and are likely correlated with other factors that impact seedling survival and composition, such as site production, overstory tree density, and decomposition rates. Second, topographic position affects seedling density, but this effect depends on elevation. Topography provides fine-scale variation in water stress as valleys catch water, increase shade, and provide shelter relative to ridges (Emanuel et al. 2011, Hoylman et al. 2018). Yet, variation at larger scales across elevation can change the relationship between topography and productivity (Hoylman et al. 2018). Thus, topography and elevation set the stage to determine seedling establishment, perhaps by controlling productive and stressful growth environments. Similarly, the proportion of pines decreased with topographic water index, which approximates soil water availability based on topographic position. As topographic water index increases, water availability likely increases, allowing more shade-tolerant species to establish and decreasing pine relative abundance. Overall, these results suggest managers should consider how the small-scale effects of topography are modulated by larger-scale changes in elevation and how this complex interaction guides the tradeoff between productivity and competition.

Conclusions

Ultimately, climate and soil interact to control establishment, survival, and growth of plants in the Sierra Nevada primarily through water limitation; however, biotic interactions strongly influence whether the dominant life forms will be trees or shrubs after a wildfire. Understanding how to shift the balance between trees and shrubs will be critical for implementing successful forest restoration and useful for prioritizing sites with limited resources. We recommend that managers prioritize planting tree seedlings the year after fire in the most productive locations, where shrubs will grow quickly and outcompete seedlings. Planting early also has the greatest impact on increasing representation of pines during forest regeneration. The web-based tool that we developed based on our results will help managers to prioritize the timing and locations of active plantings to increase reforestation efficiency following future wildfires.

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Appendix B: List of Publications, Presentations, & Delivery Products

Publication

Sorenson, Q. M., Young, D. J. N., Latimer, A. M. “Tree planting outcomes after severe wildfire depend on climate, competition, and priority: where competition with shrubs is intense, trees need a head start.” *In Review* at Ecological Applications.

Presentations

Young, D. J. N., Sorenson, Q. M., Latimer, A. M. 2019. Active and passive post-fire restoration under changing environmental conditions. Association for Fire Ecology 8th International Fire Ecology and Management Congress.

Sorenson, Q. M., Young, D. J. N., Latimer, A. M. 2020. Tree planting the year following high severity wildfire gives tree seedlings a critical head start when competition from shrubs is intense. Ecological Society of America Annual Meeting.

Sorenson, Q. M., Young, D. J. N., Latimer, A. M. 2020. Where and when to plant trees after fire in the face of water limitation and shrub competition. Natural Areas Association Annual Meeting.

Webinar

Sorenson, Q. M., Young, D. J. N., Latimer, A. M. 2020. Environmental drivers of reforestation outcomes: field-based observations and a web-based tool for prioritizing planting. California Fire Science Consortium.

Tool

Young, D. J. N., Sorenson, Q. M., Latimer, A. M. 2020. Post-fire Reforestation Success Estimation Tool (PReSET). <https://reforestation.shinyapps.io/preset/>

Appendix C: Metadata

The data collected through this project reflect the biophysical characteristics of 212 11.3 m radius circular plots that were surveyed following wildfires that burned in yellow pine and mixed-conifer forests in the Sierra Nevada of California. It includes plot-level variables representing vegetation attributes (e.g., percent cover by shrubs, density of tree seedlings, and distance to seed trees), abiotic attributes (e.g., temperature, precipitation, and solar radiation), and plot status/information (e.g., fire name, pair ID, identity as planted or unplanted). The dataset is accompanied by metadata following the “FGDC Biological Data Profile” standard of the Content Standard for Digital Geospatial Data (FGDC-STD-001.1-1999). The data and metadata will be archived in the Dryad Digital Repository upon publication of a peer-reviewed paper presenting the data.